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Deconstructing human-shaped treelines: Microsite topography and distance to seed source control *Pinus nigra* colonization of treeless areas in the Italian Apennines

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1 **Deconstructing human-shaped treelines: microsite topography and**
2 **distance to seed source control *Pinus nigra* colonization of treeless**
3 **areas in the Italian Apennines**

4

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22 **Keywords**

23

24 Anthropogenic treeline, black pine, pasture abandonment, pine recruitment, Mediterranean
25 mountains

26

27 **Highlights**

- 28 • Land-use changes can trigger tree colonization in high-elevation grasslands.
- 29 • Rapid recruitment and high tree growth rates facilitate treeline upward shift.
- 30 • Microsite topography and distance from pine plantations influence treeline dynamics.
- 31 • *Pinus nigra* treelines in Italy can respond quickly to the future global change.

32

33 **Abstract**

34 Human-shaped treelines are a common feature in mountain landscapes across Europe, and
35 particularly in secularly managed Mediterranean high-elevation areas. The abandonment of
36 traditional land use, and especially the reduction in grazing pressure at high elevations, triggered
37 secondary succession in treeless grassland areas, and favored the upward shift of anthropogenic
38 treelines in some cases. We investigated this process in four anthropogenic treeline ecotone sites in
39 the Central Apennines, Italy, populated by European black pine (*Pinus nigra* Arn.). The upward
40 treeline shift was controlled by microsite topography and the proximity to plantations acting as seed
41 source. We found a 50% probability of producing cones in trees with basal diameters of 15–25 cm,
42 heights of 2–5 m and ages of 20–25 years. The role played by climate on growth and the recruitment
43 processes seems to be secondary, or could be masked by human-shaped processes. The presence of
44 reproductive age trees at the treeline, mainly growing on debris-rich and steep slope sites, could
45 indicate that the recruitment process will increase in future, leading to patchy tree patterns at
46 different elevations. The high growth and encroachment rates observed at these human-shaped
47 treelines would indicate that general growth dynamics are speeding up, including the tree
48 colonization of treeless areas. These succession processes could cause a significant long-term
49 decline in plant diversity in species-rich grasslands. Nonetheless, tree encroachment could increase
50 forest protection against landslides and avalanches in the context of global change.

51

52 **1. Introduction**

53 Alpine treeline ecotones are sensitive indicators when assessing the ecological effects of two
54 global-change components on forests, namely climate warming and land-use modification (Harsch
55 and Bader 2011). The greater sensitivity of these high altitude tree populations to temperature
56 variability confirms that growth and tree recruitment in these marginal populations respond to
57 climate variation (Daniels and Veblen 2004, Camarero and Gutiérrez 2004). However, climate
58 warming is only one aspect of global change that may affect the location of treelines (Holtmeier and
59 Broll 2005). If traditional human activities near the treeline are common (Körner 2012), the forest-
60 grassland ecotones are usually affected by changes in the anthropogenic disturbance regimes (
61 Batllori and Gutiérrez 2008, Woods 2014).

62 Anthropogenic treelines develop under severe human impact that alters site conditions, such
63 as forest clearing, fire or livestock grazing (Holtmeier and Broll 2005). Moreover, land-use shifts
64 can severely influence treeline physiognomy masking or reversing the response of treelines to
65 climate warming (Harsch and Bader 2011, Woods 2014). Although land use is more frequently
66 associated with an abrupt transition from forested to treeless areas, different treeline types and
67 structures may be the result of various past human influences (Batllori and Gutiérrez 2008, Harsch
68 and Bader 2011). Land-use changes are long-term broad-scale disturbances and should be
69 considered as major drivers of treeline formation in human-disturbed mountain areas (Foster et al.
70 1998). Their effects on treeline dynamics can persist long after the abandonment of human activities
71 (Camarero et al. 2017, Gimmi et al. 2008).

72 During the past century, European mountains experienced rapid and extensive changes in
73 land-cover and landscape patterns which facilitated woody plant invasions in formerly grass-
74 dominated ecosystems and also upward shifts in treelines (Hofgaard 1997, Chauchard et al. 2007,
75 Gehrig-Fasel et al. 2007, Ameztegui et al. 2010, Treml et al. 2016). In southern Europe, the rapid
76 industrialization of the mid-20th century triggered deep socio-economic shifts, including a massive
77 rural exodus toward cities and the decline of traditional practices in mountains that had been based

78 on small-scale agriculture, pastoralism and forest resource utilization (Blondel and Aronson, 1999).
79 In the northern Mediterranean Basin, traditional land uses (grazing, forest and forest-floor
80 exploitation) in mountain areas became unsustainable during the 20th century and rapidly
81 abandoned (Debussche et al., 1999). Land abandonment and/or the reduction of grazing pressure
82 were often followed by national forest plantation programs which increased the surface area of
83 mountain forests and, in some cases, fostered tree invasion in old-field pasture lands (Chauchard et
84 al. 2007).

85 The Apennines are a mountainous range extending for 1200 km NW-SE across Italy with
86 numerous peaks higher than 2000 m a.s.l. (maximum elevation Mt. Corno Grande 2912 m a.s.l.).
87 The vegetation zones of the Apennines have been severely shaped by climate change and millenary
88 human activities, and now are mainly covered by deciduous forests and woodlands. European beech
89 (*Fagus sylvatica* L.) is the main species of the mountainous zone ranging from 800-900 m to 1700-
90 1800 m and forming the treeline at most sites (Vitali et al. 2017. Submitted). In Paleo and Neolithic
91 times, high-elevation Apennine forests (1900-2200 m a.s.l.) were extensively cleared for hunting of
92 wild herbivores and were transformed into wood pastures or grasslands (Piermattei et al. 2014). In
93 the central Apennines, the decrease of agro pastoral exploitation and the migration of rural
94 populations toward urban areas increased during the last 60 years (Falcucci et al. 2007). These
95 changes, together with climate warming, enhanced tree encroachment and forest expansion at high
96 elevations (Dibari et al. 2015). European black pine (*Pinus nigra* Arn.) was extensively used in
97 mountain plantations during the 20th century reforestation programs for landslide and erosion
98 control due to its pioneering character and fast land cover capacity (Isajev et al. 2004, Piermattei et
99 al. 2016). Black pine revealed a natural inclination to expand on treeless areas above the closed
100 forest limit exclusively on the limestone soils of central Apennines, reaching unexpectedly high
101 elevations (> 2000 m a.s.l.) and suggesting the formation of new and higher treeline ecotones
102 (Piermattei et al. 2012, 2014, 2016).

103 Black pine was more dynamic and expanded upslope more rapidly than most of the other
104 woody species (*Juniperus* species, *Rhamnus alpina*, *Fagus sylvatica*) in the central Apennines. This
105 process could rearrange anthropogenic treelines and timberlines (*sensu* Körner 2012) ecotones
106 above secularly disturbed mountain forests. This upslope spread of black pine could be regarded as
107 an “advance guard” of a conifer-dominated anthropogenic treeline (Piermattei et al. 2012). The
108 black pine upward expansion started 30-40 years ago and its spatial distribution at higher elevations
109 generally appeared random with no evident patterns (Piermattei et al. 2012) or even over-dispersed
110 along the slope (Piermattei et al. 2016). The radial growth of planted black pine is particularly
111 sensitive to maximum temperatures and water availability during the growing season forming
112 numerous intra-annual density fluctuations (IADF) (Piermattei et al. 2014). In a recent study in the
113 central Apennines the spatial pattern of black pine encroachment revealed that its expansion pattern
114 is independent of site location and local disturbance histories (Piermattei et al. 2016). This process
115 of secondary succession is considered to be complex and depends on several factors such as
116 mast occurrence, seed availability and dispersal, suitability of regeneration niches (*sensu* Grubb
117 1977), growth rates and tree establishment (Piermattei et al. 2012, 2016). Some of these variables
118 are linked to tree growth rates, and could be enhanced by the observed temperature increase
119 (Camarero et al. 2017). Nevertheless, site micro-topography is a major factor in treeline dynamics
120 since concave and wind-sheltered lee slopes can promote the formation of thick and long-lasting
121 snowpack, affecting tree establishment (Hagedorn et al. 2014, Kullman and Öberg 2009).

122 We investigated a recent process leading to a treeline upshift, testing the predicting role of
123 microsite topography and the distance of individual trees from neighboring black pine plantations
124 acting as seed sources. We tested whether trees that had encroached at the higher elevations in the
125 late 20th century acted as a secondary source of regeneration. We also investigated how tree size and
126 age could influence cone production which would facilitate in turn the ascent of new individuals
127 and the treeline (Piermattei et al. 2016). We used tree height rather than tree diameter because
128 height is the variable that defines treeline position and determines the tree uncoupling from soil

129 microclimate conditions (Körner 2012). Finally, we compared the microhabitat type closely around
130 the seedlings or saplings (classes defined by tree height), assuming that saplings ground vegetation
131 is influenced by vegetation dynamics under the influence of established trees.

132 In particular with this study, we searched for answers to the following questions: (i) are
133 there differences between seedlings and saplings vegetation ground-cover?; (ii) what are the main
134 abiotic variables affecting tree growth in these treeline populations?; (iii) is there a minimum
135 reproductive age threshold for newly encroached pines?; and (iv) does microsite topography and/or
136 the presence of cone-producing trees allow tree encroachment to be successfully predicted? We
137 hypothesized that microsite topography and distance to seed sources were the main factors
138 influencing the black pine colonization process at high elevation, and that this expansion process
139 could be spatially aggregated.

140

141 **2. Materials and Methods**

142

143 *2.1 Study sites*

144 We sampled four mountain treeline ecotones situated in the central Apennines (Italy). Sites were
145 located in the Marche (Mt. Bove, hereafter BOV site) and Abruzzo regions (Mt. Ocre, OCR; Mt.
146 Morrone, MOR; Mt. Genzana, GEN), where black pine encroachment is widespread (Tables 1 and
147 2; supporting information, Figure A1). We selected the sampling sites after examining and
148 interpreting aerial photographs and then carried out field visits. Selected sites fulfilled three
149 requirements: i) the presence of a timberline located over 1500 m; ii) the existence of mountain
150 peaks with elevation higher than 2000 m a.s.l. and iii) the potentiality of the upward shift up to the
151 mountain peak without geomorphological constrains. Field data was collected between 2013 and
152 2015 within altitudinal transects (width 50 m and variable length) running from the timberline up to
153 the uppermost black pine tree (Figure 1). All sampled area surfaces range from 2.25 to 4.50 ha
154 (Table 1). We regarded the timberline as the upper limit of a closed canopy forest (tree cover > 50
155 %), either broadleaf natural forest or conifer plantation, and the treeline as the highest elevation
156 where we found trees with height > 2 m. All study sites were included in different types of
157 protected areas: BOV is located in the Sibillini Mountains National Park, OCR in the Mount Ocre-
158 Acquazzese State Forest, MOR in the Majella National Park, and GEN in the Natural Reserve of
159 Mts. Genzana and Alto Gizio.

160

Site	Latitude (N°)	Longitude (E°)	Timberline elevation (m a.s.l.)	Treeline elevation (m a.s.l.)	Slope aspect	Mean slope angle (%)	Surveyed surface area (ha)
BOV	42° 54'	13° 11'	1715	1809	SW	49	3.60
OCR	42° 15'	13° 27'	1635	1708	NE	54	2.25
MOR	42° 06'	13° 57'	1542	1900	SW	32	4.50
GEN	41° 56'	13° 53'	1705	2016	SW	30	4.50

161

162 **Table 1.** Main features of the study sites. *Timberline* is the upper limit of a closed canopy forest (tree cover >
163 50 %). *Treeline* is the altitude of the upper sampled tree with a height ≥ 2 m. The growing season length was
164 set from May to September.
165



166
167 **Figure 1.** Upward encroachment of European black pine (*Pinus nigra*) trees at Mt. Bove site (BOV). A pine
168 plantation acting as seed source is visible on the left. .
169

170 Livestock grazing, especially by sheep, cows, and more recently horses, was the most
171 important human-induced pressure at all four sites. Grazing intensity has decreased significantly
172 over the last 40 years in the study region (Santilocchi and D'Ottavio, 2005). Past uncontrolled
173 intensive grazing caused widespread slope erosion that required extensive pine plantations between
174 the 1950s and 1970s. Today, less disturbed treeline ecotones are formed by forests and woodlands
175 of European beech (*Fagus sylvatica* L.) along the Apennines, and by species-rich dry grasslands
176 dominated by *Sesleria*, *Bromus* and *Festuca* species (Halada et al. 2011). All study areas are mainly

177 located on calcareous bedrock. They share a temperate oceanic climate (Rivas-Martinez et al. 2004)
178 with a Mediterranean influence characterized by summer drought downwards and the main
179 precipitation peaks in spring and autumn. Summer precipitation is not a limiting factor for treeline
180 shift since it increases upwards as in other mountain chains (Körner 2012). Snowfall is more
181 common and abundant in late winter to early spring, especially from February to the end of March
182 (De Bellis et al. 2010). The mean growing season (May to September) temperatures at the four sites
183 are 11-13 °C ($SD \pm 3$ °C), with extreme mean values ranging from 7° to 16 °C.

184

185 2.2 Field sampling

186 We mapped 429 *Pinus nigra* trees that had encroached above the timberline with a Trimble Pro 6H
187 GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential correction through
188 Pathfinder Office 4.2 software was performed with a 0.5-m estimated accuracy. We measured basal
189 stem diameter, total height and counted the number of cones for each individual pine (Table 2). To
190 characterize the regeneration niche of seedlings and saplings, we quantified the percentage cover of
191 microhabitat types (rock, debris, grass and shrub) within a circular plot with a 0.5 m radius around
192 each pine stem. The age of all the trees with a basal stem diameter ≥ 4 cm was determined after the
193 extraction of one basal increment core. For trees with a basal stem diameter < 4 cm we counted the
194 number of annual internodes (terminal bud scars) along the main stem to estimate their age
195 (Camarero and Gutiérrez 1999). We classified trees as seedlings (tree height < 2 m) and saplings
196 (height ≥ 2 m), respectively.

197

198

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201

Site	No. trees	Tree density (N° ha ⁻¹)	No. sampled cores	Trees with cones (%)	Seedlings / saplings (%)	Mean basal diameter ± SD (cm)	Mean height ± SD (m)	Mean age ± SD (years)
BOV	228	63	71	4	87 / 13	6 ± 7	1.09 ± 1.36	10 ± 5
OCR	39	17	23	26	77 / 23	9 ± 7	1.41 ± 1.23	16 ± 6
MOR	113	25	84	23	54 / 46	11 ± 6	1.81 ± 1.03	16 ± 5
GEN	49	11	35	24	67 / 33	11 ± 9	2.08 ± 2.42	17 ± 8

202

203 **Table 2.** Main structural variables of the sampled black pine (*Pinus nigra*) trees that had encroached the four
204 study sites. Seedlings are trees with height ≤ 2 m; saplings are trees with height ≥ 2 m.

205

206 We estimated the competition index for each sampled tree by calculating a distance-
207 dependent competition index at the individual scale, taking into account the number and size of the
208 neighboring competitors and their distance to the focal tree (Hegyi, 1974). We calculated the
209 competition index as the sum of the diameter quotients obtained for all the neighboring trees located
210 within a 2-m radius from the focal tree, divided by the distance between focal trees and
211 neighborhoods. We corrected edge effects by omitting trees with distances from the plot limits of
212 lower than 2 m from the calculation.

213

214 2.3 Topographic, climatic and microsite ground-cover data

215 Topographic variables were extracted from the 10-m-resolution DEM for the Italian territory
216 (Tarquini et al. 2012) for each pixel covering the mapped altitudinal transects. Specifically, we
217 calculated: i) the slope; ii) the north-eastness index with values ranging between -1 (sunniest
218 exposure) and $+1$ (shadiest exposure) and iii) the plan curvature index perpendicular to the
219 maximum slope and ranging from -1 (concave) to $+1$ (convex). Mean monthly temperatures for the
220 period 1950-2015 were obtained using the procedure reported in Carturan et al. (2016) and in
221 Brunetti et al. (2012). In the field, we assessed the seedling and saplings ground-cover, according to
222 four cover types: grass, shrub, debris, and bare rock. We compared these ground-cover proportions

223 in each site, to detect significant differences, considering that saplings can have a higher influence
224 on the ground vegetation than seedlings, during their growing process.

225

226 *2.4 Growth data*

227 We collected 213 basal cores from trees located at four treeline ecotones (Table 2). Cores were
228 mounted and glued on wooden supports, and then thoroughly polished with progressively finer
229 sandpaper until the tree rings were clearly visible. We used the semi-automatic LINTAB system
230 and WinTSAP (Rinntech, Heidelberg, Germany) to measure tree-ring width at 0.01 mm precision.
231 Most of the ring-width series were too short (< 30 years), and did not allow for a robust statistical
232 verification but only visual crossdating. Tree-ring widths were converted into basal area increments
233 (BAI) since this variable reflects growth changes more accurately (Biondi and Qeadan, 2008).

234

235 *2.5 Statistical analyses*

236 We used χ^2 tests to compare seedlings and saplings microsites at each site. We used Generalized
237 Linear Models (GLM) to predict the probability of cone production as a function of several relevant
238 variables (stem diameter, tree height and age). The goodness of fit of the GLM models was assessed
239 using McFadden's pseudo- R^2 values (Venables and Ripley 2002).

240 We fitted linear mixed-effect models (LME) to radial growth data at each site considering
241 pine trees as random factors. We applied the autoregressive process (AR(1)) which describes the in-
242 tree correlation structure of radial growth which was quantified as basal area increment. We
243 considered the following as fixed factors in the LMEs: basal diameter, year, elevation, ground
244 curvature, competition index and mean spring monthly temperatures (March April and May) that
245 can play a crucial role at the beginning of the growing season. We ranked all the potential models
246 according to the Akaike Information Criterion (AIC) and then selected the most parsimonious
247 models showing the lowest AIC value (Burnham and Anderson, 2002). We also used the Akaike
248 weights (W_i) of each model to measure the conditional probability of the candidate model assuming

249 it was the best one. We assessed the fit of the models by graphical examination of the residual and
250 fitted values (Zuur et al. 2010).

251 Finally, we fitted negative binomial GLMs to predict the number of pines (the density of
252 pines in 100 m² subplots) as a function of four topographic variables (elevation difference from
253 plantation, slope, north-eastness and curvature indices). These models were ranked according to
254 their AIC values and we selected the best ones (Burnham and Anderson, 2002). Then we applied
255 the Akaike weights (W_i) to each model (Zuur et al., 2010).

256 All statistical analyses were run using the R package (R Core Team 2016). Model selection
257 was performed using the MuMIn package (Barton, 2013). The ‘lme’ function of the *nlme* package
258 was used to fit the LMEs (Pinheiro et al., 2016). The ‘glm.nb’ function of the *mass* package was
259 used to fit the GLMs (Venables and Ripley 2002).

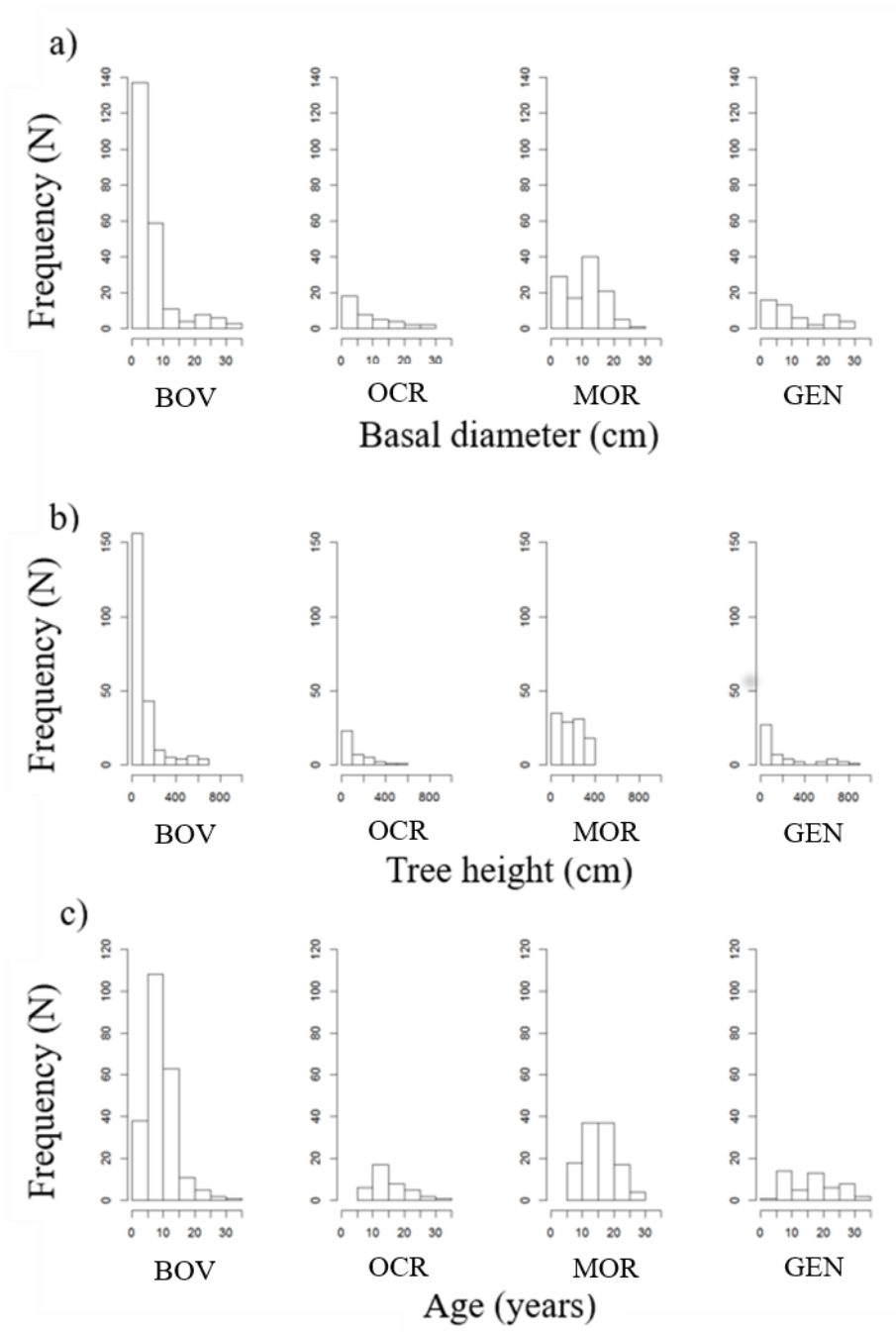
260

261 **3. Results**

262 *3.1 Size and age of treeline trees*

263 Mean timberline elevation was 1650 m and ranged between 1542 m (MOR) and 1715 m a.s.l.
264 (BOV), whilst the mean treeline elevation was 1858 m and ranged between 1708 m (OCR) and
265 2016 m (GEN) (Table 1). Black pine colonization across the treeline ecotone was scattered since
266 tree density showed a wide range of values, from 11 to 63 trees ha⁻¹ (Table 2). On average, these
267 recruited pines corresponded to 71% and 29% of seedlings and saplings, respectively. Overall, the
268 average tree size was small, with lower values at the BOV site and higher values at the GEN site.
269 The mean basal diameter was 9 cm, the mean height was 1.60 m, and the mean age was 15 years
270 (Table 2). Most sampled trees had basal diameters of lower than 15 cm and heights of lower than 2
271 m (Figure 2). On average, trees took 10-15 years to reach a height of 2 m (Supporting Information,
272 Figure A2). Modal age values varied between 5 and 20 years. The oldest trees suggested that
273 colonization started at least 30 years ago (1985–1990).

274



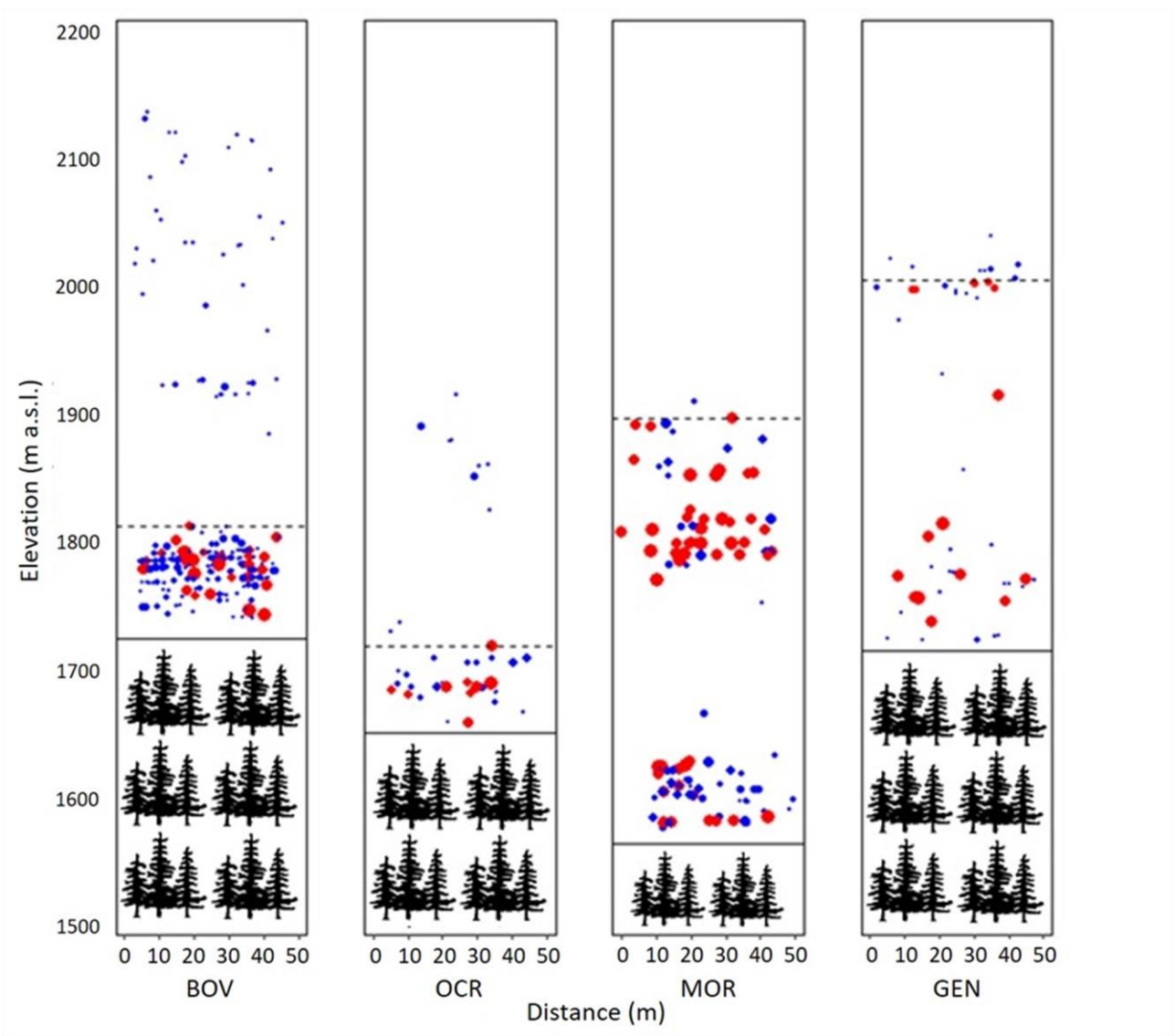
277 **Figure 2.** Frequency distribution of basal diameter (a), tree height (b) and estimated age (c) of the treeline
278 black pines (*Pinus nigra*) sampled at each of the four study sites.

280 *3.2 Treeline structure and regeneration niche*

281 Tree density decreased with altitude and distance from the pine plantations at most of the sites
282 (Figure 3), but tree height and age did not. A negative correlation of tree height with altitude was

283 observed only at BOV ($r = -0.22$, $p < 0.05$). On the other hand, there were significant and positive
 284 correlation values between altitude and tree height and age at the MOR site (both variables $r = 0.36$
 285 $p < 0.05$). Generally, the pine encroachment pattern across the treeline ecotones was not spatially
 286 structured in cohorts, but some clustered patterns were detected at 200 m intervals. These spots with
 287 higher tree density occur usually with increasing slope and consequently debris cover. Whereas in
 288 moderate slopes the grass-cover treeless areas increased.

289



290

291 **Figure 3.** Mapped point patterns of black pine individuals at the four Apennines treeline ecotones (see Tables 1 and 2
 292 for site characteristics). Blue dots are seedlings (tree height < 2 m) and red dots are saplings (height ≥ 2 m.). The dot
 293 scale size is proportional to the tree height. Solid and dashed lines correspond to the current timberline and treeline
 294 positions, respectively (*sensu* Körner 2012).

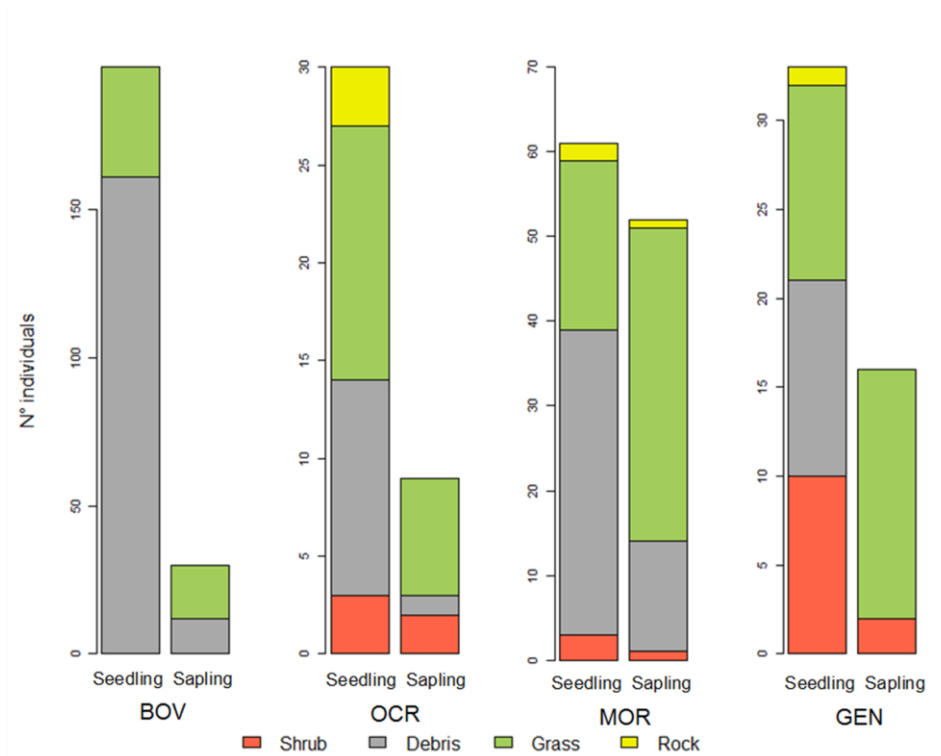
295 The negative binomial GLMs fitted to tree density showed that this variable decreased as the
 296 elevation and distance to the pine plantation increased at all sites but at GEN (Table 3). A steeper
 297 slope was also positively linked to tree encroachment at the BOV and MOR sites, whilst a higher
 298 north-eastness index (cooler conditions) was negatively related to tree density at the BOV and GEN
 299 sites.

Site	Parameters	<i>Wi</i>
BOV	− 8.48 Pla + 4.96 Slo − 2.41 NE	0.44
OCR	− 4.29 Pla °°	0.34
MOR	+ 2.89 Slo − 1.88 Pla	0.26
GEN	− 2.37 NE	0.26

300
 301 **Table 3.** Summary of the negative binomial generalized linear models fitted to black pine density as a
 302 function of topographic variables (elevation, slope, north-eastness index). The last column shows the relative
 303 Akaike weights (*Wi*). Variable abbreviations: Pla, elevation difference from pine plantation; Slo, slope; NE,
 304 north-eastness index; °°, not-significant parameters

305
 306 We detected significant differences in ground cover types of seedlings and saplings at all
 307 sites ($\chi^2 = 13.41 - 22.10$, $p < 0.01$ in all cases), except for the OCR site ($\chi^2 = 3.95$, $p = 0.27$). Most
 308 mapped seedlings were found on debris microsites, whereas most saplings were found on grass
 309 microsites (Figure 4). The most relevant difference between seedlings and saplings microsites was
 310 the very lower proportion of debris cover in saplings sites.

311



312

313 **Figure 4.** Number of black pine recruits sampled at each treeline ecotone (BOV, OCR, MOR and GEN sites)
 314 and classified as a function of their height (seedling and sapling; see Figure 3) and microsite types (shrub,
 315 debris, grass and rock).

316

317 3.3 Growth trends

318 Basal-area increment (BAI) data showed high recent growth rates ($5-10 \text{ cm}^2 \text{ yr}^{-1}$), and narrow rings
 319 were formed one year later in response to the warm-dry summer conditions observed in 2003, 2007
 320 and 2011 (Supporting Information, Figure A3). LMEs fitted to BAI data showed that tree age and
 321 basal diameter were the most important predictors of growth, whereas elevation and mean spring
 322 temperatures played a minor role (Table 4). Neither the curvature nor the competition indices were
 323 selected as growth predictors in any of the best-fitted models.

324

325

326

327

Site	Parameters	Wi
BOV	18.66 Age + 3.45 Diam + 2.86 Tm	0.77
OCR	7.60 Age + 3.45 Diam + 2.86 Tm	0.79
MOR	14.99 Age + 9.73 Diam	0.78
GEN	12.95 Diam + 9.82 Age + 3.73 Tm	0.80

328

329 **Table 4.** Summary of the linear mixed-effect models of tree growth (basal area increment) fitted as a function of site,
330 topographic variables (elevation and curvature index), tree variables (age, basal diameter, and competition index), and
331 climate variables. All regression intercepts are significant. The last column shows the relative Akaike weights (*Wi*).
332 Variable abbreviations: Age, age of tree; Diam, basal diameter; Tm, mean spring temperature (March, April and May).
333 Variables not included in the best-fitted models: Elev, elevation; Ci, Competition index; Curv, Curvature index.

334

335 3.4 Production of cones by treeline trees

336 At each site, 19% of trees produced cones (Table 2). All sites showed common tree size and age
337 characteristics when they reached a 50% probability of producing cones: 15–25 cm of basal
338 diameter, 2–5 m of tree height, and 15–25 years in age (Supporting Information, Figure A4). The
339 GLMs of cone production showed higher pseudo- R^2 values with basal diameter ($R^2 = 0.38–0.55$) or
340 height ($R^2 = 0.37–0.75$) as predictors rather than using age ($R^2 = 0.12–0.47$) (Table 5).

341

McFadden's pseudo- R^2				
Site	Degrees of freedom	Basal diameter	Height	Age
BOV	226	0.47	0.37	0.32
OCR	37	0.49	0.59	0.12
MOR	111	0.38	0.34	0.16
GEN	47	0.55	0.75	0.47

342

343 **Table 5.** Results of the Generalized Linear Models (GLMs) applied for the prediction of cone production by black pine
344 at the four study sites (BOV, OCR, MOR and GEN) as a function of tree basal diameter, height and age.

345

346 4. Discussion

347 We described the natural ascent of human-shaped treelines in the central Apennines. Black pine is
348 expanding upwards in formerly treeless areas, particularly on steep slopes and where seed
349 availability depends on downslope pine plantations. The irregular structures found at all sites
350 could also be affected by un-stationary mortality caused by climate extreme events, e.g. frosts,
351 winter drought (Camarero et al. 2015, Barros et al. 2017), or other factors such as pathogens or
352 mass wasting processes (e.g. rock fall, debris flow, land slide). We observed a patchy pattern
353 (Figure 4) of treeline shift driven by both changes in microtopography and availability of suitable
354 regeneration sites for black pine. Our results show that most tree seedlings were located on debris
355 ground-cover and steeper slopes, avoiding grass competition. The relative lower number of trees on
356 flat and grass-cover areas could be a consequence of herbs competition and snow accumulation on
357 late winter, particularly in convex areas (Tremblay and Chuman 2005). However, recruits that
358 overcome grass competition on less steep sites grew successfully, as confirmed by the abundance of
359 saplings on those sites. Indeed, debris microsites on steeper slopes most frequently hosted pine
360 seedlings (Figure 3), and tree encroachment was also favored at shorter distances from the pine
361 plantations (Table 4). Herbaceous vegetation, which is often dominant at many treeline ecotones,
362 exerts an important and mostly limiting impact on the establishment of tree seedlings (Loranger et
363 al. 2017). Studies on Scots pine (*Pinus sylvestris*) encroachment in Mediterranean mountain
364 grasslands showed that the physical barrier created by the herbaceous layer could hamper pine
365 regeneration and limit potential forest expansion (Castro et al. 2002). Bare soil or very sparse
366 vegetation are favourable substrates for pine recruitment (Loranger et al. 2017). Sites with
367 prevailing shrub cover and rocky outcrops were considered safe for establishment and development
368 of black pine (Piermattei et al. 2016) and for mountain pine (*Pinus uncinata*) recruitments
369 (Camarero and Gutiérrez 2007, Batllori et al. 2009). Abrupt treeline physiognomy and a decreasing
370 number of new trees (but no changes in height or age) as elevation increases are typical features of
371 anthropogenic treelines (Batllori and Gutiérrez 2008).

372 These results compare well with other treelines that have been studied in the central Apennines,
373 where the density of newly established trees decreased with elevation (Piermattei et al. 2016).

374 The general patchy pattern of the pine distribution observed at about every 200 linear meters
375 does not imply the formation of spatially segregated even-aged cohorts. We found different age and
376 size classes grouped together on the same preferred locations. We did not find any statistical
377 correlation between elevation and tree age or height, except for the positive values at the MOR site,
378 where older and taller trees are located at the highest elevations (Figure 2).

379 We observed that tree density decreased with elevation due to the increasing distance of
380 upslope encroached trees from pine plantations. This fits with a general theory where the shorter the
381 distance to old trees (the plantations in our case), the higher the reforestation rate (Tasser et al.
382 2007, Stueve et al. 2011). The higher availability of seeds is the main driver of pine colonization
383 since it helps propagules ascend higher, and potentially favors the establishment of new pine
384 individuals. Moreover, the results based on the negative binomial GLMs showed a positive slope
385 influence on tree density at least at the BOV and MOR sites (Table 3). Similar recruitment patterns
386 were found in the Southern United States where increased density was found to relate to slope and
387 proximity to the forest (Coop and Givnish 2007).

388 Our tree growth models showed the dominant role played by tree age and size in determining
389 growth rates (BAI) at the treeline, whereas spring temperatures had secondary importance.
390 Elevation, curvature and the competition index were not included in the best-fitted growth models
391 (Table 4). Tree density was relatively low in the study sites, likely excluding the competition effect
392 from the best models. The newly established pines are not growth-limited at high elevations
393 indicating that they have not reached the uppermost climatic threshold for tree growth. We did not
394 assess the role of wind disturbance and radiation stress on seedling abundance or tree growth even
395 though they can be additional abiotic constraints at the treeline (McIntire et al. 2016). Linking
396 changes of grazing intensity and individual tree growth is a big challenge since such historical
397 pastoral records are often lacking at local to regional scales, but their availability would allow more

398 precise testing of the impact of land-use changes on forest growth at high elevation and treeline
399 dynamics.

400 The fecundity of Mediterranean pines like black pines is particularly important considering
401 that they are significant pioneering and/or invasive species across many world regions (Richardson
402 and Rejmánek 2004). Our results showed that tree height or stem diameter were better predictors of
403 cone production than tree age (Table 5), and that similar thresholds for becoming reproductive
404 individuals occurred at all sites: ca. 15 cm of basal diameter, ca. 2 m of height and about 15 years of
405 age (Supporting Information, Figure A4). This agrees with Isajev et al. (2004) indicating that black
406 pine maturity is reached at 15 years old. We did not assess either seed production or seed viability
407 which can be relevant variables in the understanding of treeline encroachment since slow-growing
408 treeline standing trees or krummholz may form cones, but with few or no viable seeds (Camarero et
409 al. 2017). Generally, trees release many more seeds when conditions are dry and windy, potentially
410 increasing the proportion of long-distance dispersal events (Coutts et al. 2012). A comparison
411 showed that non-native black pine populations had a higher net reproductive rate and higher
412 effective dispersal than native Scots pine, leading to a rapid expansion of black pine into grasslands
413 (Debain et al., 2007). If recently encroached trees overcome bottlenecks related to seed viability, the
414 future of these anthropogenic treeline ecotones will depend on the future dynamics of successful
415 high-density tree groups or clustered islands. These trees growing on debris-rich and steep slope
416 sites may become new seed sources and catalyze the recruitment process, increasing the annual seed
417 production at closer distances.

418 The establishment of trees into treeless, high-elevation areas could become widespread in
419 many European mountains where there has been a consistent decline in human land-use and
420 traditional agro pastoral practices (MacDonald et al. 2000, Chauchard et al. 2007, Gellrich et al.
421 2007), combined with the absence of relevant geomorphological constraints (Leonelli et al. 2011).
422 These tree encroachment and forest re-growth processes may have relevant impacts on ecosystem
423 processes, influencing biogeochemical cycles, carbon sequestration and cycling, soil properties and

424 ecohydrological processes (Rundel et al. 2014). These successional processes could lead to
425 biodiversity problems since they can cause significant long-term declines in plant diversity in
426 species-rich calcareous grasslands (Dullinger et al. 2003). On the other hand, tree encroachment
427 could improve protection against landslides and avalanches (Holtmeier and Broll 2005). We need a
428 better characterization and understanding of these encroachment processes to predict the pace and
429 pattern of human-shaped treeline rebuilding.

430

431 **5. Conclusions**

432 We investigated the patterns and processes of the recent encroachment of black pine cohorts taking
433 place at various anthropogenic treelines in the Central Apennines due to the abandonment of
434 traditional land-uses. Treeline encroachment was mainly driven by microsite topography and the
435 presence of nearby seed sources (pine plantations). Overall, the high growth rates found at high
436 elevation and the rapid and often clustered encroachment patterns indicate that these human-shaped
437 treelines can also respond quickly to the future global change.

438

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Supporting Information - Appendix A

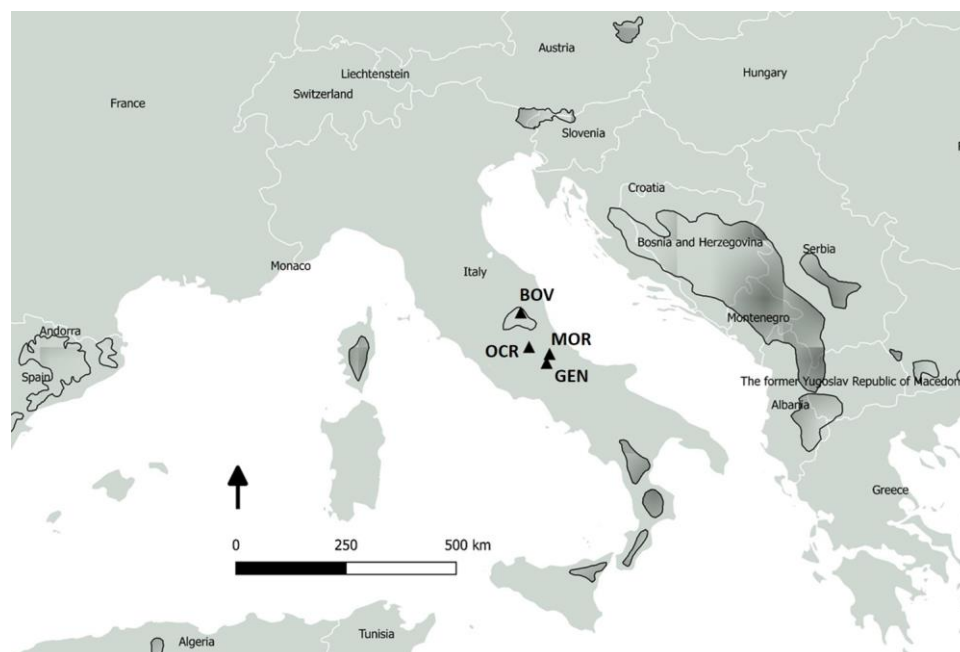


Figure A1. Natural distribution range of European black pine (*Pinus nigra* and sub-species) in the circum-mediterranean areas (black contours); locations of the four study treeline sites at the central Apennines, Italy (black triangles).

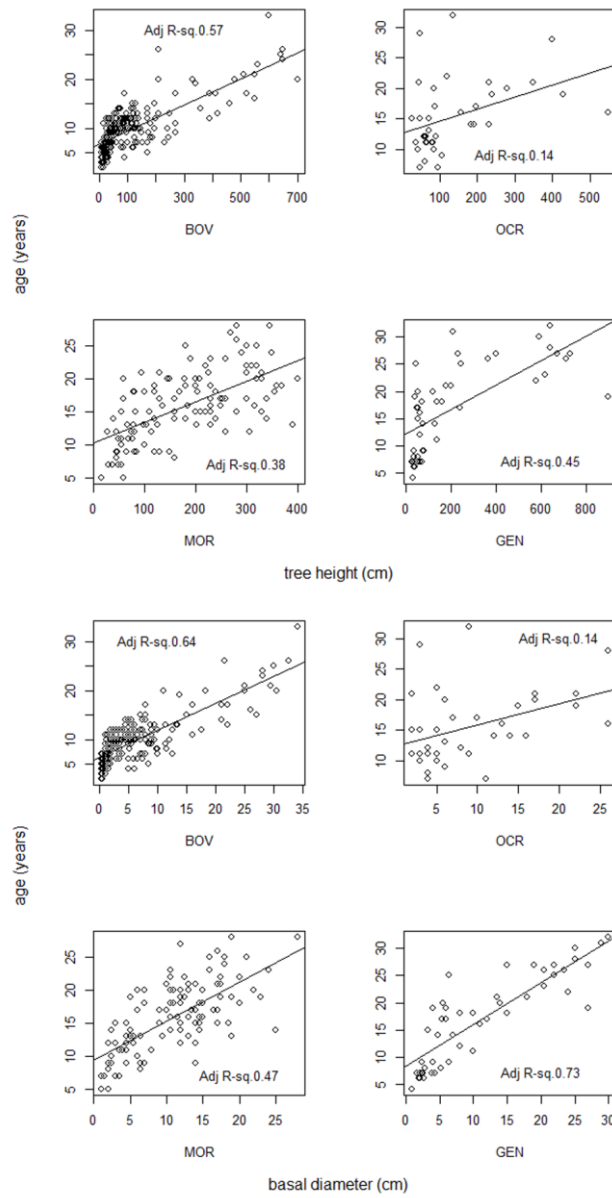


Figure A2. Adjusted R^2 values and linear regressions calculated for models of tree age as a function of basal diameter and tree height in the four black pine treeline sites.

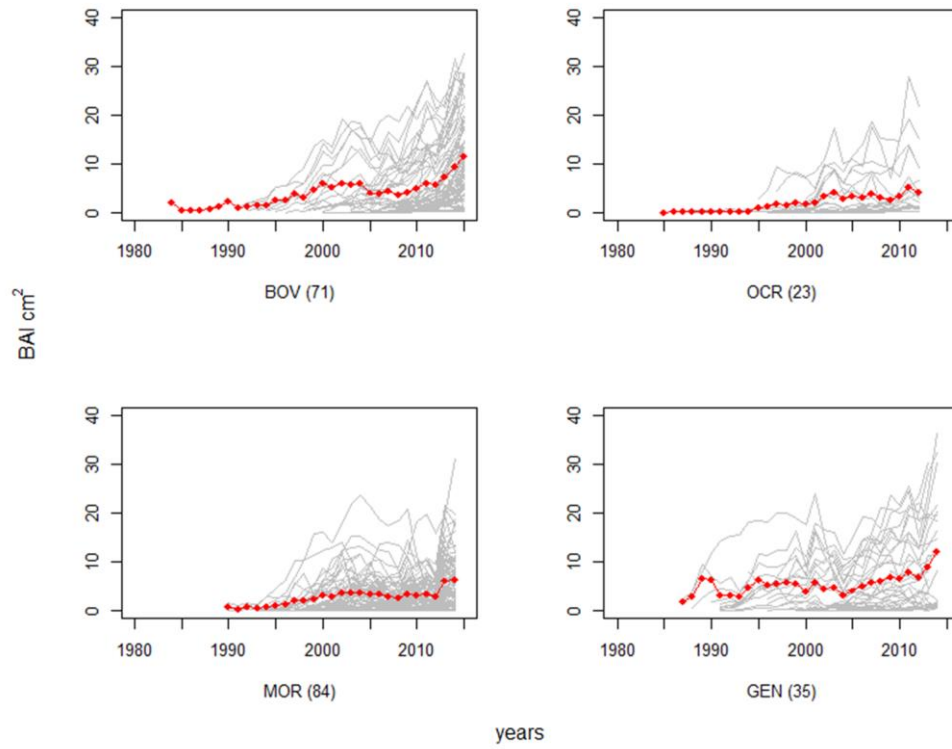


Figure A3. Radial-growth trends of black pine (*Pinus nigra*) at the four treeline sites expressed as basal area increment (BAI). Grey lines are individual series and red lines are the means of each. The numbers in brackets on the x-axis label are the number of analyzed cores at each site.

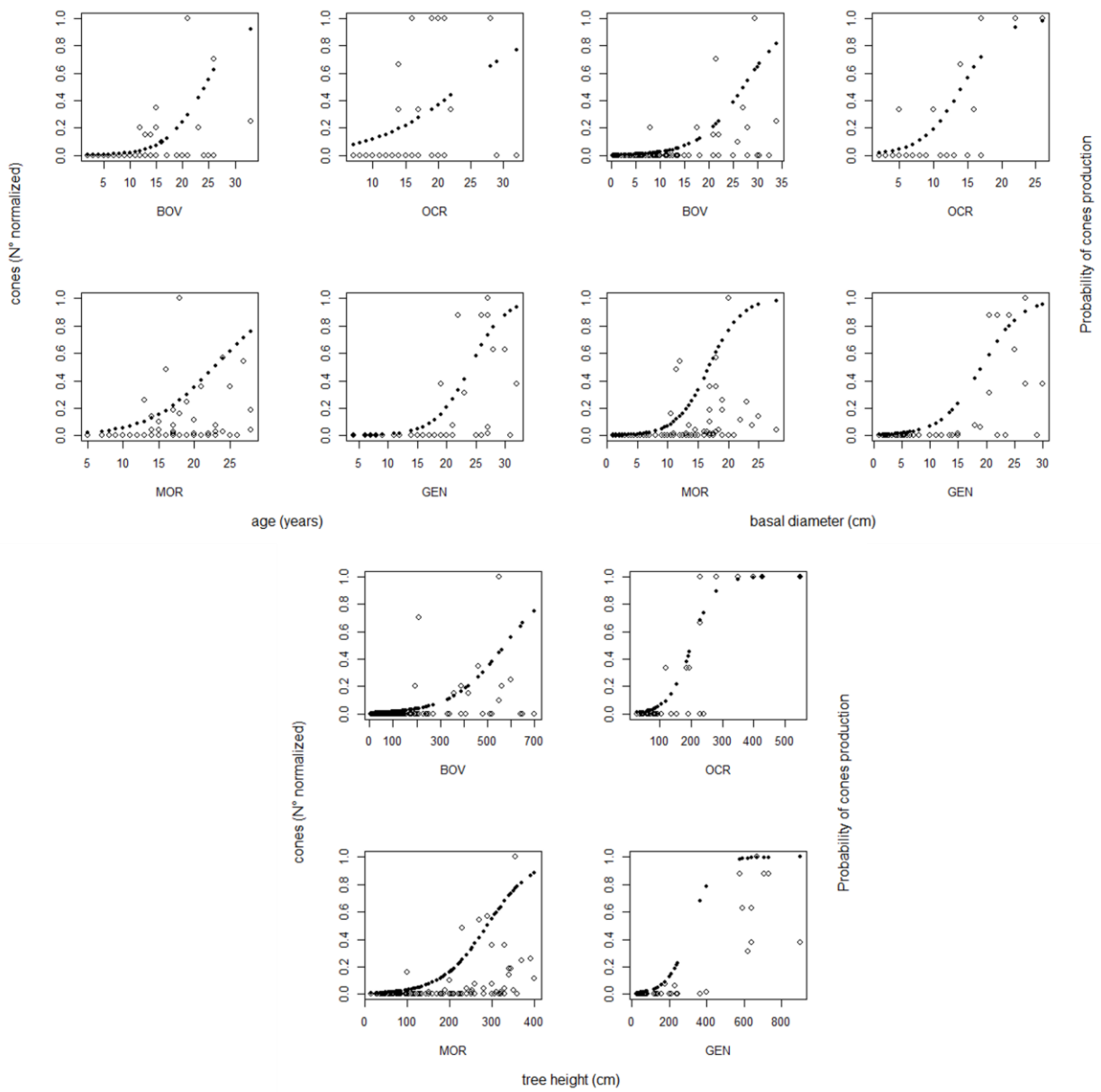


Figure A4. Generalized Linear Models (GLMs, black symbols) fitted to cone numbers (normalized values) to predict the probability of cone production in treeline black pine trees as a function of tree age, basal diameter and height.